EXCLUSION OF *ARTEMISIA TRIDENTATA* NUTT. FROM HYDROTHERMALLY ALTERED ROCK BY LOW PHOSPHORUS AVAILABILITY

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RESUMEN

Artemisia tridentata (sagebrush), la especie vegetal dominante en el desierto de Great Basin en Sierra Nevada (EEUU), es excluida en los suelos formados por la alteración hidrotermal de la roca madre. Para testar la hipótesis de que deficiencias nutricionales impiden el crecimiento de esta especie en este tipo de suelo, sometimos a plántulas de *Artemisia tridentata* a los siguientes tratamientos en un diseño factorial completo: media fuerza solución Hoagland's con N, media fuerza solución Hoagland's con P, ó media fuerza solución Hoagland's con pH 8.5 modificado mediante la adición de $NaHCO_3$. La tasa de crecimiento de las plántulas fué significativamente más alta con los tratamientos que contenían P, mientras que no tuvo ningún efecto los tratamientos con N o $NaHCO_3$. Nuestros resultados sugieren que *Artemisia tridentata* podía estar excluida de los suelos formados a partir de roca madre alterada hidrotermalmente debido a la baja disponibilidad de fósforo en este tipo de suelos.

ABSTRACT

Artemisia tridentata (sagebrush), the dominant plant species in the Great Basin desert of Sierra Nevada (USA), is excluded from soils derived from hydrothermally altered rock in this environment. To test for nutritional deficiencies for growth of sagebrush in this type of soil, we applied to sagebrush seedlings one of the following treatments in a full factorial design: half-strength Hoagland's plus N, half-strength Hoagland's plus P, or Hoagland's solution with pH modified to 8.5 by addition of $NaHCO_3$. The growth rate of seedlings was significantly highest in the P treatment, with no effect in the N or $NaHCO_3$ treatments. Our results suggest that sagebrush may be excluded from hydrothermally altered soil by low P availability.

A striking example of abrupt discontinuity in plant distribution is the occurrence of islands of Sierran conifers (*Pinus ponderosa* Laws. and *P. jeffreyi* Grev. and Balf) surrounded by a regional matrix of sagebrush vegetation (*Artemisia tridentata* Nutt.) in the Great Basin Desert of Sierra Nevada (Billings 1950; Schlesinger et al. 1989). These unique islands are found on soils derived from hydrothermally altered andesite. Soils on altered bedrock are shallow lithic entisols,

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which are light colored, very acid (pH 3.3–5.5) and low in exchangeable bases and phosphorus (Billings 1950; Salisbury 1954, 1964; Schlesinger et al. 1989). The adjacent soils derived from unaltered andesite are xerollic Haplargids which are brown, slightly basic, and high in exchangeable bases and phosphorus.

Sierran pines growing on these sites are excluded from the typical desert soils by competition for water with the more drought-tolerant sagebrush vegetation (DeLucia et al. 1988; DeLucia and Schlesinger 1991). Conversely, sagebrush is presumably excluded from the pine stands by intolerance of the low-nutrient conditions of soils derived from hydrothermally altered rock (Billings 1950; Schlesinger et al. 1989). We tested the response of sagebrush seedlings growing in altered soils to N and P additions and to modified pH. Our hypothesis was that sagebrush is excluded from hydrothermally altered rock zones by low phosphorus availability.

Materials and Methods

A greenhouse experiment was carried out in the Phytotron of Duke University. Seeds of *Artemisia tridentata* were planted in 350-mL, 7-cm diameter pots containing field soils collected from an area of hydrothermally altered rock. Three seeds were planted per pot, and seedlings were thinned to one per pot soon after emergence. Seedlings were watered daily.

To test for deficiencies in the ability of the soil to supply adequate nutrients for growth of sagebrush, we designed a 3-way factorial experiment. Twelve plants were randomly assigned to each of 8 groups, and three times each week each group received one of the following treatments in a full factorial design: half-strength Hoagland's + N, half strength Hoagland's + P, or Hoagland's solution with pH modified to 8.5 by addition of $NaHCO_3$. *Artemisia tridentata* seeds were also planted in unaltered soil to serve as a control. Plants were maintained at 25°C day and 15°C night temperature. After 40 days, plants were harvested, rinsed gently with distilled water to remove adhering soil particles, separated into roots and shoots, and dried at 70°C for 48 h before been weighed. Growth rate was determined by dividing the dry matter production by the duration of the growth period. Tissues of the 12 plants in each treatment was pooled to form one sample of shoot and one sample of root for N and P analysis. Tissues were digested in a Technicon block digester with a H_2SO_4-H_2O_2 flux (Lowther 1980) and analyzed for total N and P on a Traacs 800 autoanalyzer using standard methods. ANOVA (log-transformed data; type III sum of squares) was used to analyze treatment effects.

TABLE 1. SOIL CHEMICAL PROPERTIES ON ALTERED AND UNALTERED PARENT MATERIALS IN THE SAGEBRUSH ZONE OF THE GREAT BASIN. All data are means with 1 SE in parentheses; t-tests were used to distinguish differences between soil types. Asterisks indicate significance at $P < 0.05$. HCO_3^--P is a determination of available P from extraction at pH 8.5. (From Schlesinger et al. 1989).

Location	pH in 0.01 mol/L $CaCl_2$	HCO_3^--P(μg/g)	C (mg/g)	N (mg/g)
Unaltered	6.55*	31.4*	0.078	0.006
	(0.17)	(4.4)	(0.012)	(0.001)
Altered	3.74	5.6	0.115	0.009
	(0.15)	(2.9)	(0.015)	(0.002)

RESULTS

Some chemical properties on altered and unaltered parent materials are shown in Table 1. Average extractable P and soil pH was significantly higher in unaltered soil.

The growth rate of whole seedlings was significantly highest in the P treatment ($P < 0.0001$, Fig. 1, Table 2). Similar results were observed for root and shoot growth rate (Table 2). Total and shoot growth rate were also significantly enhanced by N additions ($P < 0.05$, Table 2), largely as a result of significantly greater growth of the seedlings when N was combined with P. When only N or $NaHCO_3$ was added to the soils there was no growth response. The $NaHCO_3$ treatment effectively increased the pH of soil solution from 3.8 to around 5.5. It is interesting to note that growth rate of sagebrush in unaltered soil was 13.54 mg/day ± 1.86 SE, significantly higher than that seen with additions of N and P to altered soil.

Although our pooling of samples precluded a statistical analysis of the differences in the N and P content of plant tissues, non P-fertilized seedlings had a P concentration ranging between 0.09% and 0.11% (Table 3). When P was added to the nutrient solution, P content ranged between 0.16% and 0.42%. Less striking differences were found in N concentration between treatments (from 1.1% to 2.3% in non N-fertilized seedlings, and from 1.91 to 3.5% in N-fertilized plants). N-to-P ratio in tissue varied between 13 and 31 in non P-fertilized and from 6.49 to 9.3 in P-fertilized plants, closer to the N-to-P ratio of 5.6 that we found in seedlings growing in unaltered soil. Even if N was not added to the watering solution, N uptake was highest in P-fertilized seedlings (Table 4).

DISCUSSION

The results indicated that P, but not N was a primary factor limiting the growth of sagebrush in altered soils. We expected that additions of $NaHCO_3$ might increase the availability of P in the soils

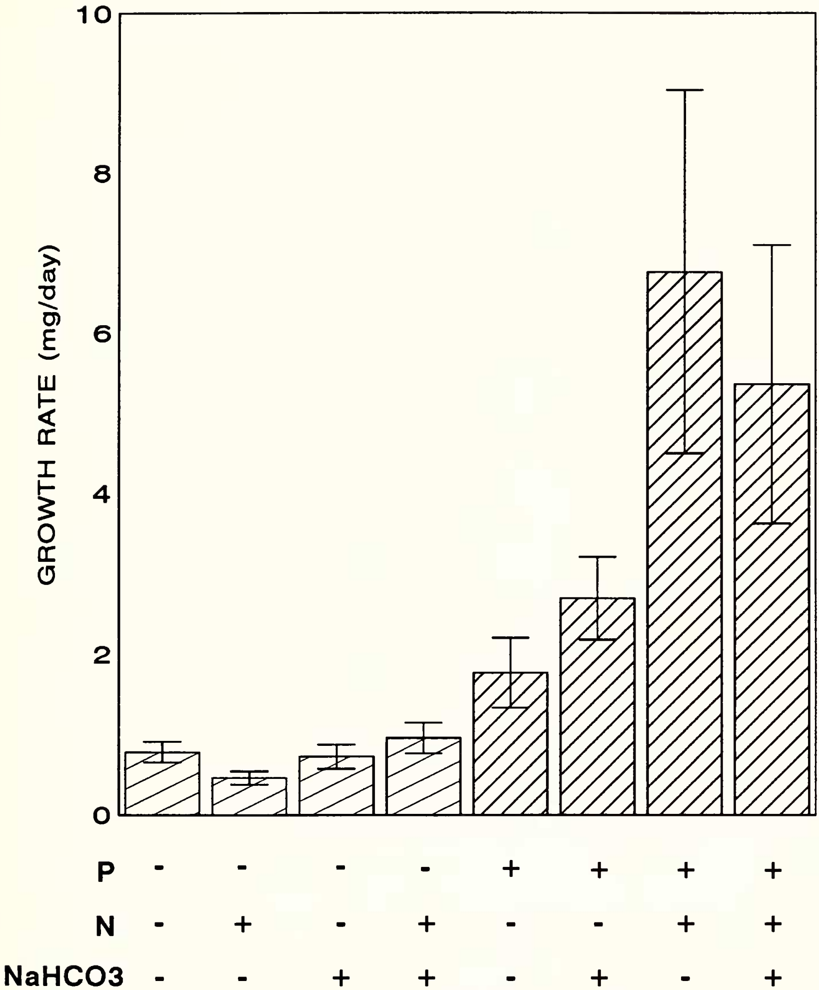

FIG. 1. Growth rate of *Artemsia tridentata* seedlings grown under N, P and $NaHCO_3$ treatments in soils derived from hydrothermally altered soils. Bars are 2, SE.

derived from hydrothermally altered rock, because the solubility of phosphorus is restricted by Fe and Al minerals at low pH (Schlesinger 1991). However, we found no effect of $NaHCO_3$ on inherent low P content in soils derived from hydrothermally altered rock. The lack of response of plant growth to our $NaHCO_3$ treatments suggests that low pH *per se* is not a factor that excludes *Artemisia tridentata* from soils derived from hydrothermally altered rock. A different hypothesis is that the inability of sagebrush to grow in the altered soil might be due to high Al^{3+} concentration of the soil

TABLE 2. ANALYSIS OF VARIANCE (TYPE III SUMS OF SQUARES) FOR GROWTH RATE OF *ARTEMISIA TRIDENTATA* CULTIVATED IN SOILS DERIVED FROM HYDROTHERMALLY ALTERED ROCK WITH N, P AND $NaHCO_3$ TREATMENTS.

Source	Sum of squares	df	F-ratio	Sig. level
	Total (roots + shoots)			
Main effects				
A: Nitrogen	2.56	1	4.20	0.0440
B: Phosphorus	41.59	1	21.11	0.0000
C: $NaHCO_3$	1.12	1	1.83	0.1802
Interaction				
AB	3.99	1	6.53	0.0126
AC	0.08	1	0.14	0.7155
BC	0.10	1	0.17	0.6849
ABC	2.32	1	3.80	0.0550
Residual	46.44	76		
	Roots			
Main effects				
A: Nitrogen	0.72	1	1.11	0.2947
B: Phosphorus	45.87	1	70.47	0.0000
C: $NaHCO_3$	1.20	1	1.84	0.1789
Interactions				
AB	4.68	1	7.19	0.0090
AC	0.20	1	0.31	0.5834
BC	0.13	1	0.21	0.6570
ABC	1.95	1	2.99	0.0879
Residual	49.47	76		
	Shoots			
Main effects				
A: Nitrogen	5.53	1	8.89	0.0039
B: Phosphorus	38.81	1	62.42	0.0000
C: $NaHCO_3$	1.10	1	1.78	0.1867
Interaction				
AB	3.30	1	5.32	0.0239
AC	0.01	1	0.02	0.8850
BC	0.08	1	0.12	0.7621
ABC	2.97	1	4.78	0.0319
Residual	47.25	76		

solution. Al^{3+} concentration might be reduced by phosphate application to the acid soil. However, the solubility of Al^{3+} should have also declined precipitously with additions of $NaHCO_3$ alone stimulating plant growth, but this effect was not seen in our experiment. Goldberg (1985) was able to grow *bodenvag* species on soils from hydrothermally altered rock with additions of $CaCO_3$. Addition of $CaCO_3$ increases the solution pH, but it also produces a high Ca availability that could exert important influence on some biogeo-

TABLE 3. N, P CONCENTRATION IN THE ROOT AND SHOOT TISSUE OF *ARTEMISIA TRIDENTATA* CULTIVATED IN SOIL DERIVED FROM HYDROTHERMALLY ALTERED ROCK UNDER N, P AND $NaHCO_3$ (C) TREATMENTS. (a) Root tissue in the +P treatment was not available for analysis.

Treatment	Concentration (%)		
	N	P	N:P
	ROOT		
—	1.26	0.10	12.98
+N	2.66	0.11	24.42
+C	1.37	0.11	12.82
+N+C	2.04	0.11	19.33
+P	a	a	a
+P+C	1.06	0.16	6.49
+N+P	2.09	0.25	8.34
+N+P+C	1.91	0.22	8.51
	SHOOT		
—	1.79	0.09	19.77
+N	3.03	0.10	31.03
+C	1.92	0.09	21.91
+N+C	2.47	0.10	24.39
+P	2.30	0.31	7.54
+P+C	2.23	0.30	7.55
+N+P	3.14	0.42	7.52
+N+P+C	3.48	0.37	9.30

chemical processes relevant to plant growth. For example, Lajtha and Schlesinger (1988) found that $CaCO_3$ directly inhibited the uptake or the availability of P to roots in *Larrea tridentata* seedlings. Additions of P reduced mortality of the seedlings grown in soils from hydrothermally altered rock. Only 2 seedlings (4%) died along the course of the experiment in P amended soils versus 9 seedlings (19%) in non-P amended soils.

TABLE 4. FINAL N AND P MASS (FINAL DRY WEIGHT * N OR P TISSUE CONCENTRATION) IN THE SEEDLINGS OF *ARTEMISIA TRIDENTATA* CULTIVATED IN SOIL DERIVED FROM HYDROTHERMALLY ALTERED ROCK UNDER N, P AND $NaHCO_3$ (C) TREATMENTS.

Treatment	N mass (mg)			P mass		
	Root	Shoot	Total	Root	Shoot	Total
—	0.22	0.25	0.47	0.017	0.013	0.030
+N	0.21	0.32	0.53	0.009	0.010	0.019
+C	0.21	0.26	0.47	0.017	0.012	0.029
+N+C	0.33	0.55	0.88	0.017	0.022	0.039
+P		0.70			0.093	
+P+C	0.58	1.17	1.75	0.089	0.155	0.245
+N+P	2.55	4.66	7.21	0.306	0.620	0.925
+N+P+C	1.88	4.04	5.92	0.221	0.434	0.655

There are only a few examples in which plant species are totally excluded from soils by low phosphorus availability. For example, Berliner et al. (1986) report complete exclusion of *Cistus incanus* from basaltic soils in Israel due to a failure of mycorrhizal development. Tyler and Olsson (1993) and Tyler (1994) find the calcifuge behavior of several species is due to the inability to utilize the native phosphorus of limestone soils. Our results suggest that sagebrush may be excluded from hydrothermally altered soils by low P availability which is tolerated by Sierran conifers that have higher nutrient-use efficiency and slow growth rates.

Acknowledgments

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